THE PRIMING ACTION

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Losses of carbon from a soil by priming action are given by $x-y-z$, where x is the amount of carbon lost by a soil incubated with added organsic matter, y the portion of x coming from the added organic matter and z the carbon lost by the soil incubated alone. An observed priming action may be caused by isotopic exchange, errors in calculating y from isotopic data, differences between conditions in the soil with and without organic additions, or by mechanisms as yet unknown by which the organic addition speeds up decomposition of the native soil organic matter. The priming action is almost certainly not an important factor in assessing the value of green manuring.

It is not likely that the methods of measuring priming action used in the laboratory (measurement of evolved carbon dioxide) can be applied in the field. However, by adding labelled plant material to two plots, one of which is subsequently bare fallowed and the other cropped, it should, in time, be possible to demonstrate the presence or absence of a priming action. Pending such experiments the priming action is best assumed to be zero, particularly as the laboratory work on both its magnitude and cause (or causes) cannot yet be described as conclusive.

On peut exprimer les pertes en carbone que les effets d'activation provoquent dans un sol par la formule $x-y-z$, où x est la quantité de carbone perdu par un sol incubé avec des matières organiques ajoutées, y la fraction de x provenant des matières organiques ajoutées et z la quantité de carbone perdu par le sol incubé seul. Lorsque l'on observe un effet d'activation, la cause peut en être un échange isotopique, des erreurs dans le calcul de y à partir de données isotopiques, des différences dans l'état du sol avec ou sans addition de matières organiques ou des mécanismes encore inconnus, par lesquels l'adjonction au sol de matières organiques accélère la décomposition de ses matières organiques naturelles. Il est presque certain que l'effet d'activation n'est pas un facteur important pour l'évaluation du rôle de la fumure verte.

Il est improbable que les méthodes utilisées en laboratoire pour évaluer l'effet d'activation (mesure de l'anhydride carbonique libéré) soient applicables sur le terrain. Toutefois, en ajoutant du matériel végétal marqué dans deux parcelles, dont l'une est ensuite mise en jachère nue et l'autre cultivée, il devrait être possible de démontrer, avec le temps, la présence ou l'absence d'un effet d'activation. En attendant de telles expériences, le mieux est de supposer que cet effet est égal à zéro, du fait notamment que les recherches de laboratoire sur son importance et sa ou ses causes ne peuvent être encore considérées comme concluantes.

La pérdida de carbono en un suelo debida a las acciones de iniciación viene dada por la fórmula x-y-z, donde x es la cantidad de carbono que pierde un suelo incubado con materias orgánicas añadidas; y es la fracción de x proveniente de la materia orgánica añadida; y z es la cantidad de carbono perdido por el suelo incubado solo. Una acción de iniciación o cebo puede proceder de un intercambio

isotópico, de errores en el cálculo de y, a partir de datos isotópicos, de diferencias entre las condiciones del suelo a que se han añadido materias orgánicas, y el suelo a que no se añade nada, o de mechanismos todavía desconocidos, mediante los cuales la adición de materias orgánicas acelera la descomposición de la materia orgánica natural del suelo. Es casi seguro que la acción de cebo no es un factor importante en la evaluación de la función de los abonos verdes.

No es probable que los métodos que se utilizan en laboratorio para medir la acción de iniciación (medición del anhídrido carbónico desprendido) pueden aplicarse en el terreno. No obstante, echando vegetales marcados en dos parcelas de terreno, una de las cuales se deja luego en barbecho completo y la otra se cultiva, debiera ser posible poder demostrar, en el momento oportuno, la presencia o la ausencia de una acción de cebo. Mientras dichos experimentos no se lleven a cabo, lo más conveniente será suponer que la acción de iniciación es igual a cero, especialmente teniendo en cuenta que los trabajos de laboratorio relativos a la magnitud y la causa (o causas) de tal acción no pueden considerarse todavía definitivos.

INTRODUCTION

Newly added organic matter may stimulate or retard the decomposition of organic matter already present in the soil. A change in the decomposition rate caused by fresh organic additions is described as a priming action, and may be positive or negative. Figure 1, taken

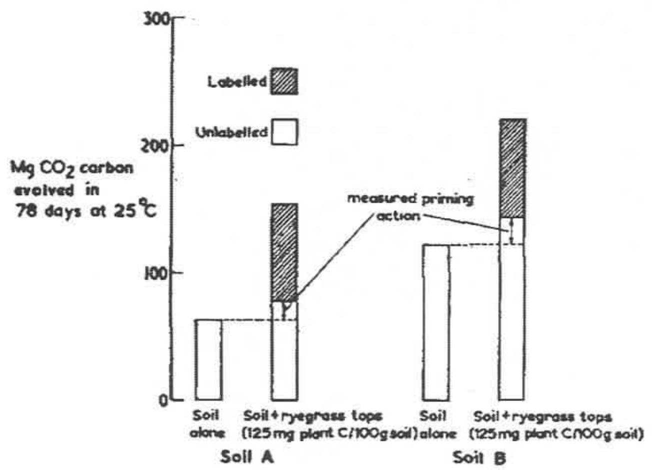

Fig. 1. The priming action

from my own work, illustrates the priming action. Two samples of soil taken at different times from the same experimental plot were incubated with uniformly labelled ryegrass. Soil *A* was taken after a year's bare fallow, soil *B* six weeks after 34 metric tons of farmyard manure per hectare, plus the stubble from the preceding wheat crop, had been ploughed in. In both soils adding ryegrass increased the rate of decomposition of the organic matter already in the soil: i.e. there was a positive priming action. The amount of organic carbon lost by priming action in a given time is $x-y-z$, where x is the total amount of carbon dioxide carbon evolved from a soil incubated with organic material, y that part of x which comes from the organic addition and z the carbon dioxide carbon evolved when the soil is incubated alone. Isotopic methods are normally used to distinguish between x and y.

This review is almost exclusively concerned with soil organic carbon. The "apparent" priming actions found when labelled inorganic nitrogen is added to a soil, and subsequent changes in labelled and unlabelled inorganic nitrogen are followed, have been thoroughly investigated by JANSSON[12] and will not be discussed here. For convenience the organic matter present in a soil before organic additions are made will be referred to as the "native" soil organic matter.

PUBLISHED WORK ON THE PRIMING ACTION

In 1926 LÖHNIS[16] concluded from the results of field and greenhouse experiments on green manuring "that the effect of growing legumes upon succeeding crops is undoubtedly not exclusively due to the manuring effect of their residues" and that intensified bacterial activ-

ity resulting from the incorporation of green manures in the soil increased the mineralization of humus nitrogen. Löhnis's interpretation of the results of his experiments was adversely criticised by PINCK and ALLISON[21]. An unequivocal demonstration of a priming action became possible only after isotopic techniques were int
BENT and NORMAN,[6] in an experiment further described by BROADBENT and BARTHOLOMEW,[5] used carbon-13 labelled plant material to demonstrate a priming action. With 2 per cent additions of sudan grass the evolution of carbon from the native soil organic matter was increased four to eleven times in incubations lasting eleven days. These are the largest priming actions ever recorded. Broadbent and Norman suggested that the process could be likened to "a forced draught on the smoldering bacterial fires of the soil". BROADBENT,[4] again using carbon-13 labelled plant material, found a positive priming action in a soil containing about 3 per cent organic matter and a negative one in a soil containing 13 per cent organic matter (including much undecomposed plant material). HALLAM and BARTHOLOMEW[11] added carbon-14 labelled plant material to three different soils at three rates of addition and found that the higher additions produced a larger priming action than the lower. With some of the smaller additions of plant material there was less carbon in the soil after incubation with plant material than in the soil incubated alone, despite the carbon remaining from the plant material added. A feature of Hallam and Bartholomew's results is the small percentage retention of plant carbon at their low rate of addition. For example, when soybean straw was applied to one soil, only 4·8 per cent of the added plant carbon remained after 119 days incubation. Such extensive decomposition in so short a time is quite unique. BINGEMAN, VARNER and MARTIN[3] investigated the decomposition of carbon-14 labelled glucose and alfalfa in an organic soil. The amount of carbon in the soil at the end of the experiment was always less when incubated alone than when incubated with organic additions. With glucose there was a negative priming action in the first few days, followed by a positive one for the remaining period of incubation. With alfalfa the effect was reversed, an initial positive priming action being followed by a negative one. However, in these experiments the alfalfa used was a composite sample, part being uniformly labelled and part being unlabelled. Supplementary experiments showed that the labelled and unlabelled alfalfa decomposed at slightly different rates so that it is difficult to interpret the priming action measurements quantitatively. STOTZKY and MORTENSEN[25] added rye to an organic soil and found that the loss of carbon by priming action was not statistically significant. They also found that the percentage loss of carbon from the plant material was the same at all levels of addition and that the soil incubated alone contained less carbon at the end than the soil incubated with plant additions. JANSSON[13] incubated carbon-14 labelled glucose with soil and found that a second addition of (unlabelled) glucose did not accelerate the decomposition of the residue from the previous glucose addition. He did, however, find that glucose additions accelerated decomposition of the native soil organic matter (10–15 per cent over that from the controls). GOSWAMI and DATTA[10] using plant material labelled by a short exposure (24 hr) to active carbon dioxide, found both positive and negative priming actions when their plant materials were incubated with a mineral soil. SØRENSEN[23] observed both positive and negative priming actions when various fractions and derivatives of labelled straw were incubated in a mineral soil. Apart from one addition which altered the pH of the soil, the

biggest increase in evolution of carbon dioxide from the native soil organic matter was 35 per cent, the biggest decrease 14 per cent.

An outstanding feature of the literature on the priming action is that it contains (with two exceptions) no data on which to judge the statistical significance of the results. Loss of carbon by priming action is given by $x-y-z$, where x, y, and z are as defined in the introduction. The measurement of each of these quantities is subject to considerable variation, however carefully the experiment is carried out. Great care is required in interpreting measurements of the loss of carbon by priming action if standard errors are not given, particularly if, as in almost all the published values for the priming action, the additional carbon lost by priming is less than half the loss of carbon from the control soil. Apart from errors due to variation between replicate incubations, systematic errors will occur if the plant material is not uniformly labelled or if the microbial environment is different in control and treated soil.

THE MECHANISM OF THE PRIMING ACTION

This section is solely concerned with mechanisms which can, either wholly or in part, explain how the addition of labelled plant material can alter, or appear to alter, the amount of carbon dioxide evolved from the native soil organic matter during incubation. Explanations of the priming action fall into four groups, (1) those setting out models which can give rise to an apparent priming action even though the decomposition rate of native soil organic matter is unaltered, (2) those based on errors in relating the amount of carbon-14 evolved to the amount of labelled plant carbon decomposed, (3) those based on the difference in environment between soil incubated with and without organic additions, and (4) those explanations postulating mechanisms by which the newly added organic matter can increase the decomposition rate of the native soil organic matter. These will be examined in turn.

(1) Systems which can give rise to an apparent priming action. Consider a soil containing unlabelled calcium carbonate to which carbon-14 labelled material is added. The labelled

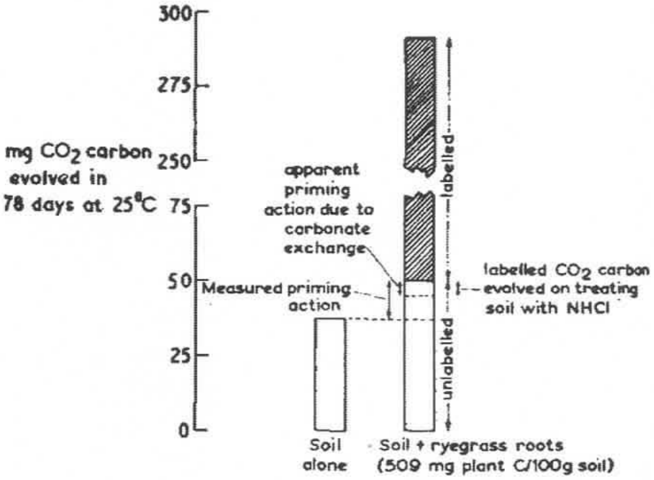

Fig. 2. Evolution of labelled and unlabelled CO_2 from a soil containing 1·3 per cent $CaCO_3$ incubated with uniformly labelled ryegrass roots.

carbon dioxide evolved by decomposition of the plant material will exchange with carbonate via soil solution bicarbonate. At the beginning of the incubation each molecule of labelled carbon dioxide exchanged will be replaced by an unlabelled one, thus increasing the evolution of unlabelled carbon dioxide at the expense of the labelled and causing an apparent priming action although the overall output of carbon dioxide from the soil plus addition is the same whether exchange takes place or not. Some of my results, shown in Fig. 2, illustrate this process. A calcareous soil was incubated with uniformly labelled ryegrass. At the end of the incubation the soil was treated with hydrochloric acid and the evolved labelled carbon dioxide determined: although the amount was not sufficient to completely account for the loss of carbon by priming

action, at least part of this loss was due to an "apparent" priming action (assuming the amount of labelled carbon present as bicarbonate at the end of the incubation to be small compared to the amount of labelled carbon evolved when the soil was treated with hydrochloric acid). This process giving rise to an

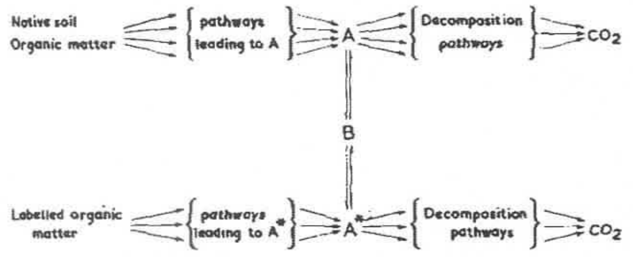

Fig. 3. Generalized decomposition scheme giving rise to an apparent priming action.

apparent priming action is a special case of a more general mechanism (Fig. 3). In Fig. 3, B can be any part of the native soil carbon which is capable of exchanging with A^*, where A^* is a chemically homogeneous pool of material produced during decomposition of the labelled addition. The larger the ratio B/A^* and the more rapid the exchange the larger will be the apparent priming action. As the incubation proceeds, A and B will move towards isotopic equilibrium with each other and the apparent priming action will tend to zero. The exchange is not necessarily inorganic: for example B can be a part of the unlabelled soil biomass exchanging unlabelled for labelled carbon dioxide by systems such as those discussed by WOOD and STJERNHOLM.[27]

(2) Priming actions caused by errors in relating the amount of carbon-14 evolved to the amount of plant carbon decomposed.

The amount of plant carbon decomposed in a given time is obtained by measuring the carbon-14 activity (or the carbon-13 enrichment) of the evolved carbon dioxide and then using a factor to convert it to plant carbon decomposed. If isotopic fractionation occurs, or if the plant carbon is not uniformly labelled an apparent priming action can result. Isotopic fractionation during humification is almost certainly small, for reasons discussed by CRAIG[8] and any apparent priming action caused by it will be too small to be observed. Only where a large fraction of the evolved carbon dioxide is re-absorbed by soil organisms[24] is isotopic fractionation likely to be important.

The factor used to convert carbon-14 activity in the evolved carbon dioxide to amount of plant carbon evolved is determined by combusting a known amount of plant material and measuring the activity of the resulting carbon dioxide. If growing plants are exposed to carbon-14 labelled carbon dioxide for a short time the water soluble fraction is more heavily labelled than the cellulose and lignin.[7] Even plants grown for almost their entire existence in labelled carbon dioxide[14] can be non-uniformly labelled, as shown in Table 1. In soil the water soluble part is most rapidly decomposed[7] and if this is also the most heavily labelled fraction, the use of a factor converting carbon-14 activity to whole plant material will give an apparent negative priming action. This will turn to a positive one as decomposition proceeds, when the more resistant (and lightly labelled) parts of the plant material are being decomposed. An effect of this sort was used by SZOLNOKI and VÁGÓ[26] to show that the water soluble portion of labelled straw was the most rapidly decomposed.

(3) Priming actions caused by differences between the microbial environments in soil incubated with and without organic matter.

Decomposing organic matter can alter the microbial environment of soil in many ways: some of the more important will be considered here. Additions of organic material can alter the pH of a soil[2] particularly when they are large relative to the amount of native organic

matter. If this happens, the soil organic matter in the sample being incubated with plant material is at a different pH from the soil organic matter in the control: as the rate decomposition of organic matter is pH dependent[2] an apparent priming action may result.

If inorganic nitrogen is immobilized by the added material, competition may occur between the native soil organic matter and the addition for inorganic nitrogen, resulting in a reduced loss of carbon dioxide from the native soil organic matter. This may be a factor where

Table 1. The Distribution of Activity in Ryegrass. The Plants were Placed in a Growth Chamber 18 days after Germination and then Exposed to Carbon Dioxide of Uniform Specific Activity for 49 days[14]

Plant part	% of total dry matter of plant	Specific activity, μc/g carbon	Standard error
Tops			
Unfractionated	100	23·8 (3)*	± 0·21
Part soluble in alcohol/benzene	10·3	—	
Part soluble in hot water	35·6	24·6 (2)	
Part soluble in 17·5% KOH	20·2	23·8 (2)	± 0·26
Insoluble residue	34·0	22·5 (2)	
Roots			
Unfractioned	100	21·0 (4)	± 0·18
Part soluble in alcohol/benzene	6·8	—	
Part soluble in hot water	24·3	23·6 (2)	
Part soluble in 17·5% KOH	19·5	20·1 (2)	± 0·26
Insoluble residue	49·4	19·4 (2)	

* Number of determinations in parenthesis

The oxygen demand of a decomposing organic addition may reduce the partial pressure of O_2 in an incubation to less than that in the control incubation if aeration is inadequate. Parr and Reuszer[19] showed that less carbon dioxide was produced from a soil incubated in an atmosphere containing 5 per cent oxygen than from an incubation in air.[19] The oxygen demand will be particularly large when readily decomposed materials such as glucose are added to soil: the negative priming actions found by Bingeman, Varner and Martin[3] immediately after additions of glucose to a muck soil may have been caused by differences in aeration between incubations with and without glucose.

organic materials of wide C/N ratio are added to soils of wide C/N ratio.

(4) Mechanisms by which organic additions can directly increase the decomposition rate of the native organic matter.

Until a loss or gain of carbon attributed to the priming action has been shown to be significant, and not explicable under headings (1), (2) and (3) above, it is unwise to speculate further on its origins. Very few of the priming actions recorded in the literature meet these conditions. However, a brief list of possible mechanisms may be useful, even if only to be eliminated by future experiments.

Soils contain microbial spores many of which

will germinate on adding fresh organic matter. A resting spore respires more slowly than a germinated one so that in this way a positive priming action may be produced. It is possible that some of the products of decomposition may either solubilize or displace some of the native soil organic matter, rendering it more decomposable.[17] The priming action may also be due to an increase in the concentration of exocellular microbial enzymes following the organic addition, resulting in more rapid breakdown of the native soil organic matter.

GREEN MANURING AND THE PRIMING ACTION

An examination of the practice of green manuring under different agricultural conditions in different parts of the world would form a topic for a whole conference. The function of this section of the review is to point out that the priming action cannot be blamed for the failure of green manuring to live up to its protagonists' expectations as a method of restoring organic carbon to soil.

Apart from certain unexplained effects of green manuring on crop yields there is a long standing controversy on its influence on soil organic matter. MANN[18] found a greater increase in carbon and nitrogen on plots receiving green manures than in the corresponding plots not receiving them. Earlier work by CROWTHER and MANN[9] on the same experimental farm had led to the conclusion that a green manuring –wheat rotation appeared to cause a more rapid loss of organic matter than continuous wheat. Conflicting evidence on this point from other parts of the world has been reviewed by JOFFE.[15] Probably the main cause of the controversy is that changes in soil organic matter resulting from green manuring are usually small relative to the total amount of organic matter in the soil. In field incubations at Rothamsted using labelled ryegrass (see Fig. 6 in the review on turnover of organic matter in soil) cut just before flowering, about one third of the plant carbon remained in the soil after one year. Using this figure, one metric ton per hectare of dry ryegrass tops would add roughly 0.006 per cent carbon to the top 15 cm of a soil, if ploughed in and left for a year, assuming a direct linear relationship between additions and losses of plant carbon. The validity of the assumption has already been examined in the review on turnover of organic matter. This calculation only holds for one plant material in one soil under one set of climatic conditions but is unlikely to be greatly in error for the normal range of green manures used in temperate zone agriculture,[20, 21] providing decomposition is not retarded by factors such as soil acidity or poor aeration.

Apart from its function as a source of new soil organic matter, green manuring can alter the decomposition rate of soil organic matter in a number of ways. ROVIRA and GREACEN[22] showed in laboratory experiments that mechanical disturbance of soil increased the rate of decomposition of soil organic matter. The increased consumption of oxygen by soil after mechanical disruption was short lived, but during the first day the oxygen demand was doubled in certain soils. The additional soil disturbance caused by preparing a seedbed, sowing and ploughing in a green manure may well increase the decomposition rate of native soil organic matter over that in a soil allowed to rest undisturbed between cultivations. Mechanical disturbanced in the laboratory[22] was almost certainly more thorough than ever achieved in field cultivation, so that the effect of a few cultivations per year is unlikely to be great.

It has been suggested, for example by HALLAM and BARTHOLOMEW,[11] that green manuring "may actually serve to accelerate the decomposition and exploitation of the carbon already there" (in soils of the prairie regions), and that

the priming action is partly responsible for this. This point of view was discussed twelve years ago by PINCK and ALLISON[21] who concluded "that the effect of green manures on the soil organic matter is of only minor practical importance". No measurements of the priming action published after Pinck and Allison's paper in 1951 have given values as high as some of those published before that date, so that there is no new evidence to modify their conclusions so far as the priming action is concerned. If green manuring reduces the level of organic matter in a soil to below that in a similar soil treated in exactly the same way except for the omission of green manuring, then the annual increment of organic matter from the green manure must be less than the annual loss of organic matter by priming action. With one partial exception[11] all of the published work on the priming action has shown that a soil incubated with plant material contains more carbon at the end of a period of incubation than the same soil incubated by itself. Priming actions may well occur in a field receiving green manures, but it would be rash to postulate on the basis of the present laboratory evidence that the annual loss of soil organic matter by priming action is greater than the amount of soil organic matter left annually by the green manures.

It is not likely that the methods of measuring priming action used in the laboratory (measurement of evolved carbon dioxide) can be applied in the field. However, by adding labelled plant material to two plots, one of which is subsequently bare fallowed and the other cropped, it should, in time, be possible to demonstrate the presence or absence of a priming action. Pending such experiments the priming action is best assumed to be zero, particularly as the laboratory work on both its magnitude and cause (or causes) cannot yet be described as conclusive.

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DISCUSSION

M. FRIED *(IAFA)*: Did your first slide represent an indictment of farmyard manure since it showed a permanent tie-up of more than 2000 kg of nitrogen?

D. S. JENKINSON *(United Kingdom)*: In this case, yes, since the average yield from the N.P.K. plot with 0·11 per cent N is not very different from that of the F.Y.M. plot which contained more than three times as much nitrogen.

H. W. SCHARPENSEEL *(Germany)*: In your sixth slide there was a big gap between the turnover rates of native soil-carbon and carbon-14 labelled ryegrass. How would these curves look if the native soil carbon and labelled humic acid from plant decomposition were compared for their residence time in the soil?

D. S. JENKINSON: I think it will be many years before the decomposition rate of the humic acid fraction of the labelled carbon falls to that of the native soil organic matter.

W. FLAIG *(Germany)*: How do you know when the organic matter in a field has reached equilibrium?

D. S. JENKINSON: To be sure that a soil has reached a steady state it is necessary to determine the organic matter content over a prolonged period. However, it is probably not essential in turnover calculations that a soil be absolutely in equilibrium; errors caused by other assumptions made in steady state calculations are probably greater than those introduced if the soil is not quite at equilibrium.

B. ULRICH *(Germany)*: Long-term field experiments are the only way to detect the effect of green manure on the carbon content of soil under field conditions. Are there any data on the effect of green manuring on the carbon content of soil?

D. S. JENKINSON: Yes, long-term green manuring experiments have been reported at Woburn in England and from a number of different parts of the world. Joffe's review in *Advances in Agronomy*, Vol. 5, 1955, lists some of them.

R. S. SWABY *(Australia)*: Is there any evidence that the addition of organic phosphorus and organic sulphur compounds prime the decomposition of humic-P and -S?

D. S. JENKINSON: No evidence. However, certain organic phosphorus compounds, for example A.T.P., may dissolve fractions of the soil organic matter in the way pyrophosphate dissolves soil organic nitrogen, thus possibly rendering them more decomposable.

S. LARSEN *(United Kingdom)*: Could an increase in soil temperature contribute to the priming effect?

D. S. JENKINSON: No, the priming action measurements I have been considering are done in the laboratory at constant temperature.

A. EVEN-HAIM *(Israel)*: Are you certain, in research on the priming effect, that the carbon-14 labelled CO_2 recovered comes from the decomposition of carbon-14 labelled matter introduced into the soil? My question is based on an observation made in the course of my work. I grew plants in a solution containing labelled vanillic acid in a chamber along with the controls which were growing in non-labelled solutions. At the end of the experiment (which took 14 days) all the control plants contained carbon-14 in their roots and stems and, furthermore, the nutrient solutions used for the controls were radioactive. Do you not think that microbial processes, or some other complex process, may bring about an exchange between carbon-14 and carbon-12 in the soil?

D. S. JENKINSON: Yes, many soil organisms possess systems capable of exchanging unlabelled for labelled carbon dioxide. This exchange can result in an apparent positive priming action. However, in my experiments, this mechanism, although operative, did not explain the whole of the observed priming action.